BRIEFER ARTICLES

THE DEVELOPMENT OF THE MACROSPORANGIUM OF YUCCA FILAMENTOSA.[1]

CONSIDERABLE attention has been called to the species of Yucca on account of the curious symbiotism existing between them and the moth (*Pronuba yuccasella*) which is the principal agent in pollinating the stigma (5, 15). The very complete studies of Riley, Trelease, Engelmann, and others have related to the process of pollination by this moth and the parallel life-histories of the two organisms. My work has been on the embryology of *Yucca filamentosa* L., and the present paper treats of the development of the macrosporangium. In many points its development does not differ from that of the other Liliaceae which have been the subject of so much embryological research; but there are certain interesting deviations which may or may not be a result of the curious life-history of the plant.

The material used was collected in the summer of 1900 from plants growing in the botanical garden of the University of Michigan, and was fixed in Flemming's weaker killing fluid and in Worcester's killing fluid.[2] The ovaries were imbedded in paraffin, sectioned, and stained upon the slide. The haematoxylin stains of Kleinenberg and Haidenhain and picro-nigrosin were very satisfactory stains for nuclear study, while Zimmermann's fuchsin-iodin-green was the best for general cytological study. I wish here to acknowledge my indebtedness to Dr. James B. Pollock for criticisms and suggestions.

The anatropous macrosporangia are arranged in six vertical rows, two in each chamber, arising in acropetal succession from a ridged placenta. A hypodermal cell is early differentiated in the apex of each macrosporangium, from which two kinds of cells later originate.

[1] LXV. Contribution from the Botanical Laboratory of the University of Michigan.

[2] As I am not aware that the formula for Worcester's killing fluid is familiar to cytologists, I give it, as follows:

Mercuric chlorid, saturated aqueous solution	96 parts
Formalin (40 per cent. formaldehyde)	4 "
Acetic acid 10 per cent.	10 "
Formic acid to each liter of solution	5 drops

Wash in 70 per cent. alcohol.

It soon divides by a periclinal wall, forming a primary tapetal cell and a sporogenous cell. The primary tapetal cell subsequently divides by two anticlinal walls at right angles to each other, forming four (rarely two) tapetal cells which closely resemble the reproductive cells in size, contents, and staining qualities (*figs. 1, 2*). Other investigators (4, 11) have noted similar processes of division in monocotyledonous plants. The sporogenous cell, by two divisions, forms an axial row of four potential macrospores; frequently these divisions occur by walls all of which are perpendicular to the long axis of the ovule (*fig. 1*), but more often the walls between a_1 and a_2 are parallel or oblique to the axis of the ovule (*fig. 2*). So far as I know, no case has been reported where four potential macrospores have the arrangement shown in *fig. 2*.

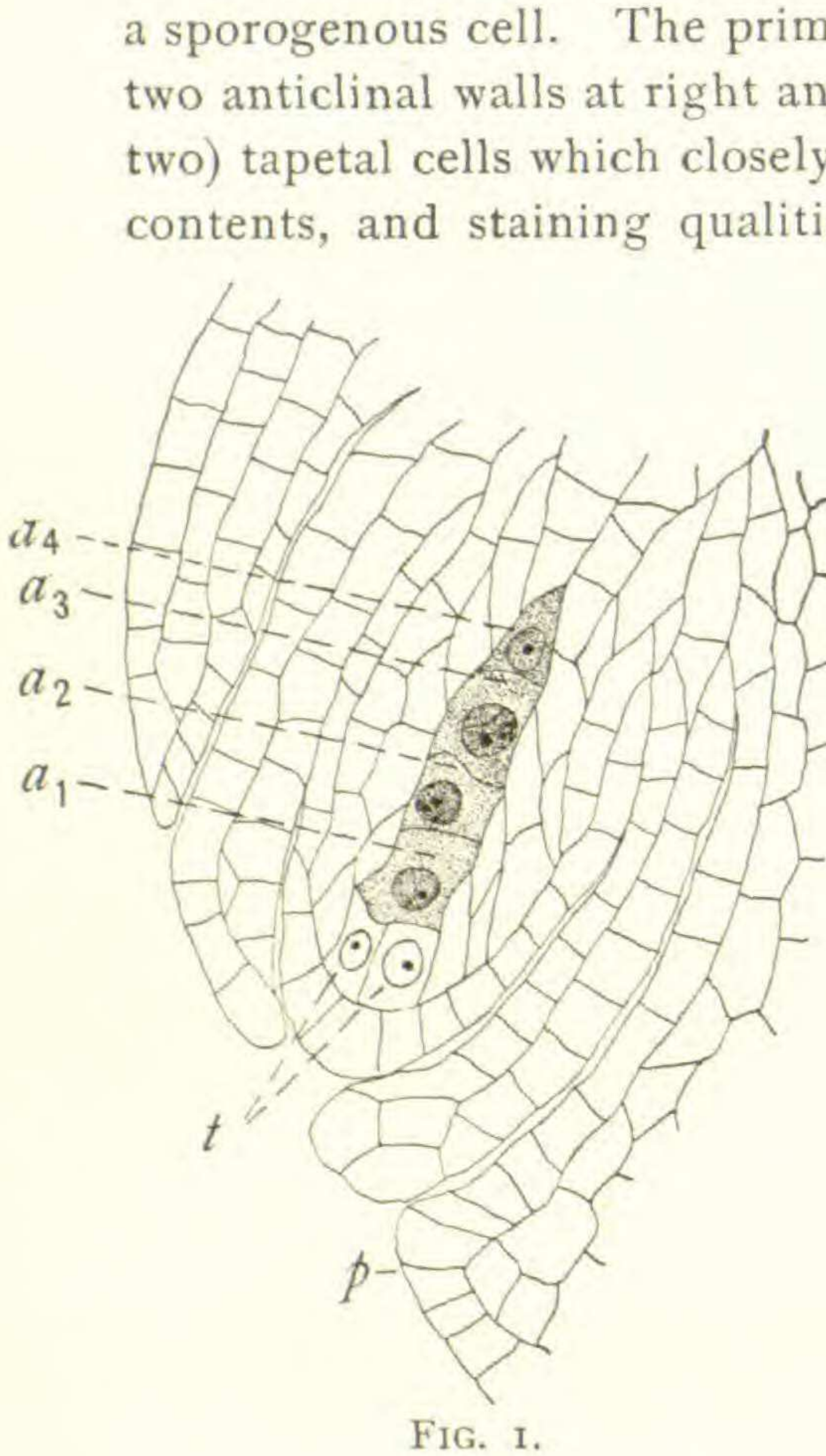

FIG. 1.

An axial row of four macrospores has been reported in a number of plants, some of the best-known cases being the Gramineae (3), many of the Rosaceae (1, 14), Elodea, Triglochin, Carex, Polygonum (3), Avena (9), Canna (11), Eichhornia, Pontederia (8), and probably in *Potamogeton natans* (12) and *Lilaea subulata* (7). Three macrospores occur in Orchis (1, 14), Allionia, Gomphrena, Geum (3), Naias and Zannichellia (6), two in *Convallaria majalis, Potamogeton foliosus* (11), and *Arisaema triphyllum* (4), except that in the last named they stand side by side instead of forming an axial row.

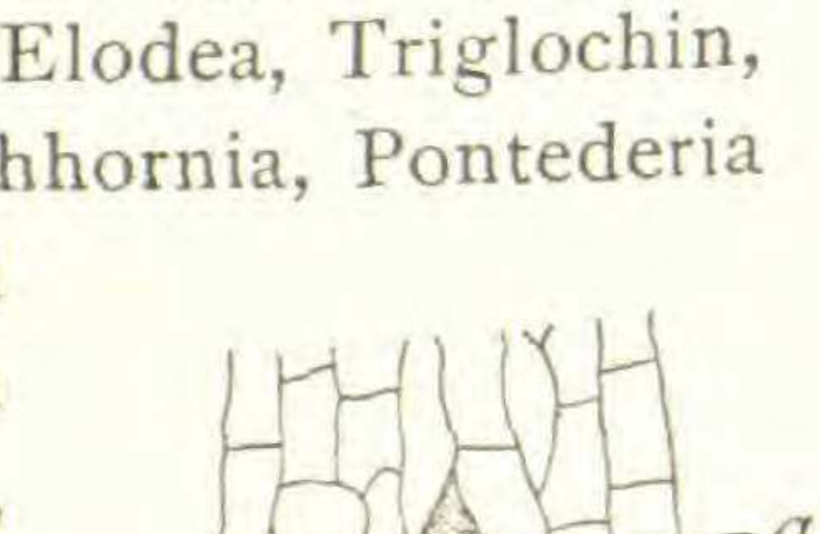

FIG. 2.

When the wall between a_1 and a_2, *fig. 2*, is nearly parallel to the plane of the section the axial row appears to have only three macrospores, but careful focusing shows that a_1 and a_2 lie one above the other. The cell at the basal end of the row is usually triangular.

Three of the cells of the row disintegrate. The survivor becomes the embryo-sac. There are indications that any one of the four macrospores may become permanent, but in every case where I could be certain, a_3 was the nucleus which matured. Zimmermann's fuchsin-iodin-green was a very valuable stain for differentiating the reproductive nuclei from the vegetative nuclei, making it possible to distinguish the two with certainty. The cell which becomes permanent is often larger than its sister cells from an early stage; as it enlarges further, their walls break down and their contents are absorbed, leaving the macrospore in a long pointed cavity in the middle of the nucellus. The process resembles that described by Strasburger (1) in *Polygonum divaricatum*.

The development of the macrosporangium in *Yucca gloriosa* has been worked out by Vesque (2), who described a hypodermal cell which gives rise to a two-layered tapetum and three potential macrospores, but did not follow the development far enough to determine which one persisted. There is no question, in all the cases which I examined, but that *Y. filamentosa* is constant in having a single layer of tapetal cells and that such cells as a_1 and a_2, *fig. 2*, are true macrospores. The fuchsin-iodin-green stain plainly differentiates the nuclei of the different cells. When disintegration begins the three macrospores disappear almost simultaneously, followed later by the tapetal cells.

FIG. 3—A young macrosporangium at the time of the formation of the haustorial tube: *e*, embryo-sac mother cell; *p*, placenta. ×360.

The permanent nucleus now enters upon the divisions which produce the eight nuclei of the embryo sac. *Fig. 3* represents the first division and shows the shape of the embryo-sac at that time. The subsequent divisions are accomplished in the lower, pointed end of the cavity. The antipodal nuclei are often separated from each other by distinct cell walls. By the time the sexual nuclei are formed, the tapetal cells and part of the nucellus have disintegrated, leaving the apical end of the embryo-sac in contact with the epidermis of the macrosporangium.

The embryo-sac grows chiefly in the apical part at the expense of the nucellus and tapetum. The basal portion of the sac appears to sink deeper into the nucellus by reason of the elongation of cells in its walls, but it increases in diameter very slightly. The result of this manner of growth is to produce a narrow tube which penetrates the nucellus nearly to the extremity of the fibrovascular bundle (*figs. 4, 5*). The migration of the nuclei into the tube and its relation to the fibrovascular system suggest that it may have a nutritive function, serving as an haustorium. This suggestion is further supported by the presence of fine granular material in the tube and in the cells adjacent to the fibrovascular bundles and the tube. If these are the granules of an organic acid, as their staining qualities indicate, or some form of plastic food material, then the migration of the nuclei may be considered a chemotactic response analogous to the growth of the pollen tube and the entrance of the antherozoids into the embryo-sac. Vesque (2, p. 304) found haustorial appendages in the embryo-sacs of Scrophulariaceae, Santalaceae, and Lathraea, and comments upon the parasitic nature of the embryo-sac in certain instances. A recent writer (13) reports the presence of haustorial appendages in certain of the Araliaceae.

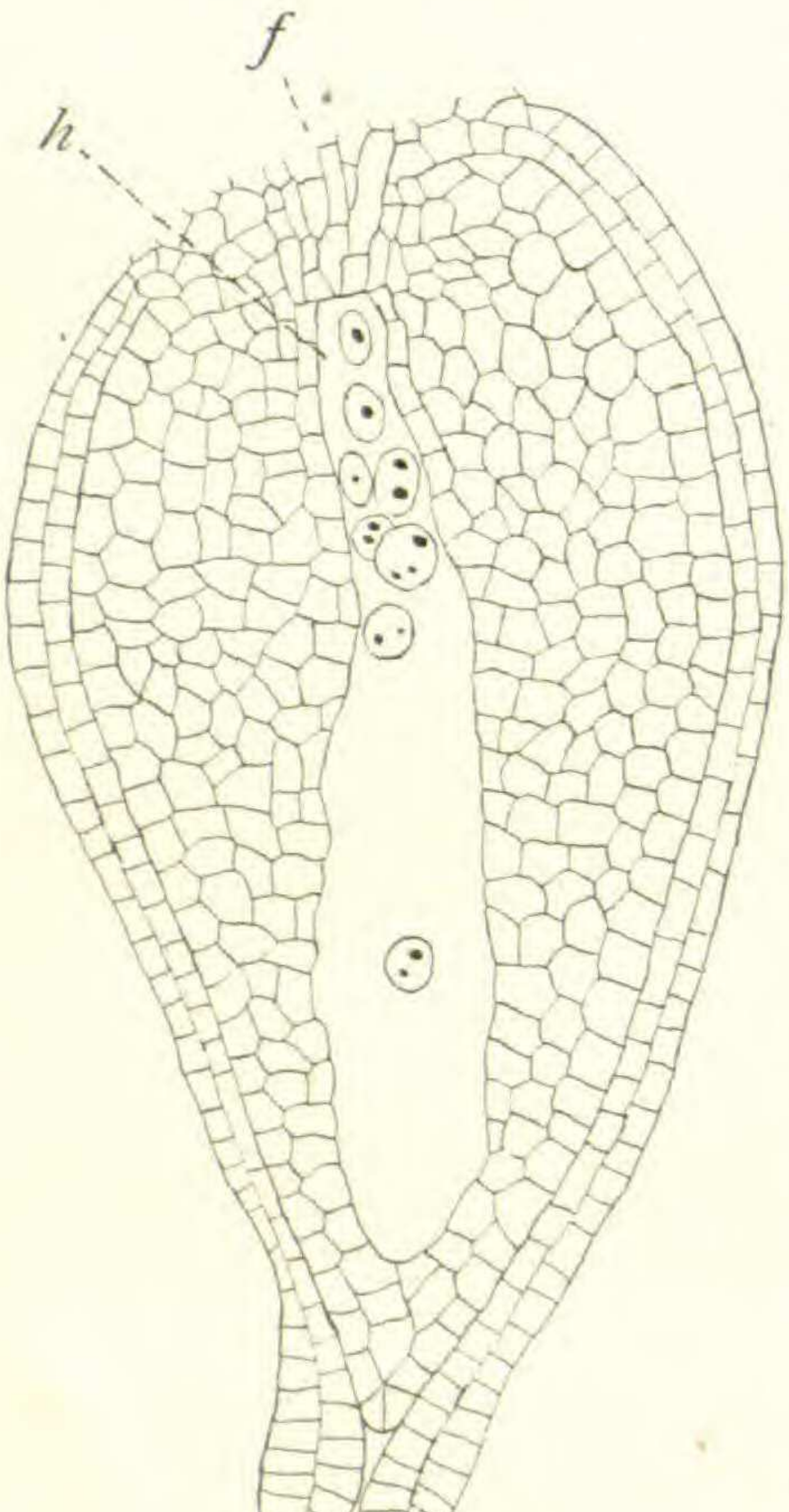

FIG. 4.—An embryo-sac in which the haustorial tube is fully formed and the divisions of the macrospore are completed: *f*, fibrovascular bundle; *h*, haustorial tube. × 360.

After the divisions of the macrospore are completed, the egg-cell and synergids move up to the apical end of the embryo-sac; the definitive nucleus also moves out, but often only to the mouth of the haustorial tube, sometimes to the middle of the embryo-sac; the antipodal nuclei usually remain in the tube.

Coincident with the divisions of the macrospore and formation of the embryo-sac haustorium, there is a rapid increase in the amount of nucellar tissue, an enlargement of the embryo-sac cavity, and a preparation for fertilization.

The columnar cells which serve as an epidermis to the placentae and to the macrosporangium are very large on that part which covers the ridges of the placentae and the basal part of the stalk of the macrosporangium. From these cells there exudes a mucilaginous secretion a short time before fertilization occurs. The secretion passes outward in the cavity surrounding the macrosporangia, often forming a hood around each macrosporangium (*fig. 5*). In passing the micropyle the secretion often finds its way into it, and may force its way for some distance between the inner and the outer integuments. The question arises: Is not this an *artifact*, caused by some fault in the technique? The methods of preparing the material were varied until there was no longer any doubt as to their reliability and the identity of the secretion whenever obtained. A somewhat similar thing has been noted by Guignard (10) in the tulip. He speaks of papillae lining the wall of the cavity surrounding the macrosporangia, among which the pollen tube makes its way to the micropyle. Campbell also mentions the presence of secreting cells on the funiculus in Naias, but found no secretion. Wherever I have seen pollen tubes in my sections they have been growing in or toward this secretion. There is no evidence that this secretion has any distinctively nutritive function in itself, but rather that it serves as a medium through which the substance capable of attracting pollen tubes diffuses outward from the micropyle. If the colloidal secretion were nutritive, there would be an attraction of the pollen tubes into all parts of the secretion, but this is not the case.

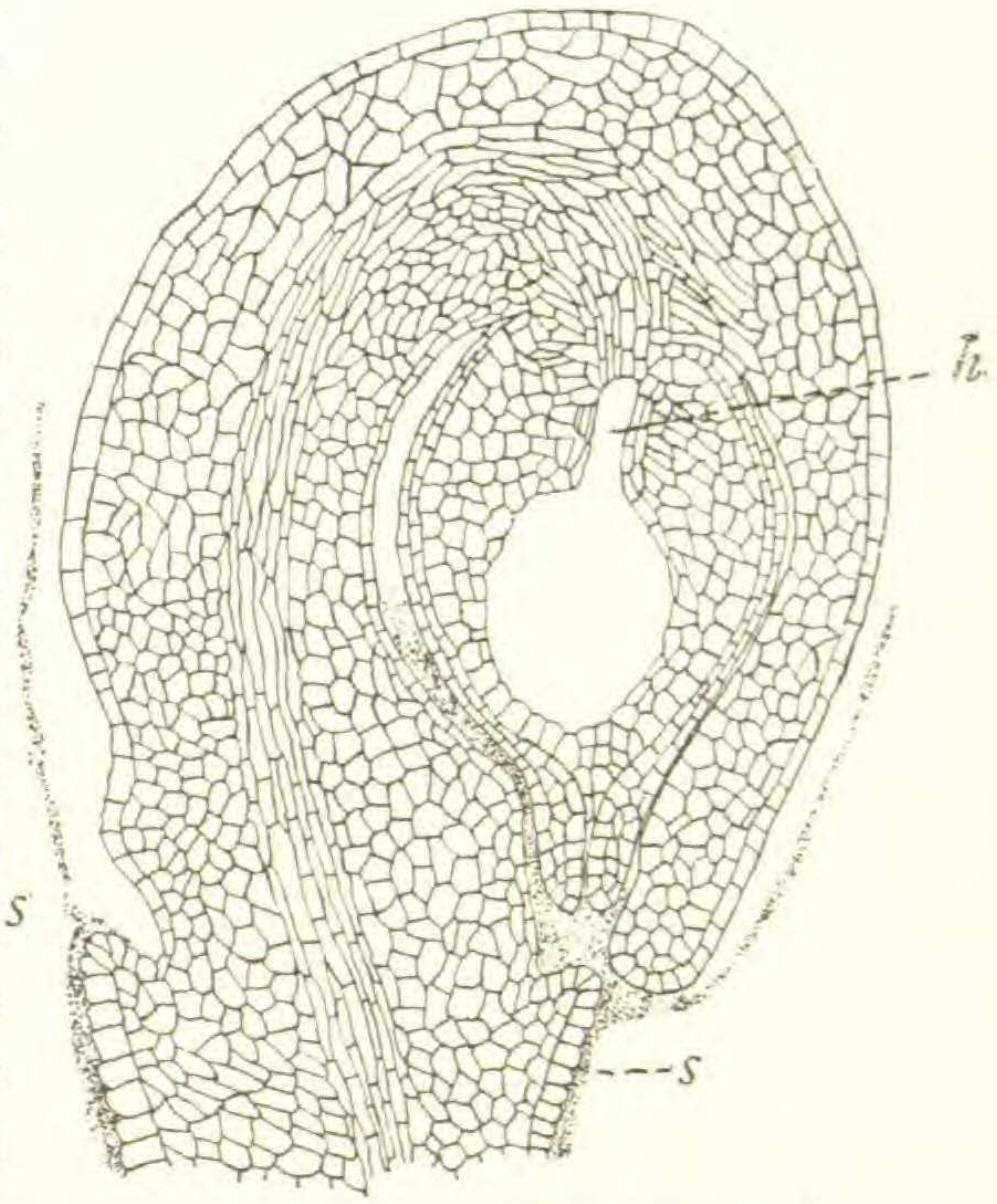

FIG. 5.—A macrosporangium at the time of fertilization: *h*, haustorial tube; *s*, secretion from placentae. × 270.

The egg cell of the embryo-sac is fertilized shortly after the formation of the secretion. The results of fertilization are several: the formation of the secretion from the placentae ceases and all which exists disappears; the small rectangular cells on either side of the haustorial tube rapidly elongate, and the embryo sac enlarges in a transverse direction.—HOWARD S. REED, *University of Michigan.*

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FAXONANTHUS.

THE January number of the BOTANICAL GAZETTE, in a review of the first part of Professor C. S. Sargent's *Trees and Shrubs*, calls attention to the fact that a new genus, *Faxonanthus*, is therein described without mention of the family to which it belongs. The author of the genus desires to say that in the transcription of the original manuscript for publication a brief note on its affinity was omitted. It may be stated that the new genus *Faxonanthus* belongs to the Scrophulariaceae, and should be placed near the genus Leucophyllum.—J. M. GREENMAN, *Gray Herbarium.*